Spring | 14

Differential habitat use as a behavioral thermoregulatory strategy in lemurs

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Abstract

In order to reduce the energetic cost of controlling internal body temperatures physiologically, animals engage in "behavioral thermoregulatory activities." These strategies include changing postures, social huddling, and moving to different levels of the forest canopy in response to environmental changes. For lemurs, behavioral thermoregulation can be especially important to be able to cope with the daily and seasonal climatic variations of their habitat because they have a lower basal metabolic rate than other primates. In this study, we analyzed the patterns of temperature and humidity variation throughout the forest at the Duke Lemur Center and then analyzed how individuals of *Propithecus coquereli* and *Lemur catta* use these variations as a strategy for behavioral thermoregulation. We found that generally temperatures tended to decrease deeper into the forest, with a few deviations from this pattern during fall, and for different forest coverage. We also found that humidity generally increased deeper into the forest, although this pattern reversed for the deciduous enclosures during the fall months. When analyzing how the lemurs use the forest in response to temperature variation, we found that contrary to what we expected, individuals preferred to spend the majority of their time at "edge" or "out" of the forest for all temperatures, and spent very little time at the interior of the forest (30m or 60m). This was also the case when we controlled for sun exposure levels. However, individuals did employ other behavioral thermoregulatory strategies, including increasing extended postures during hotter temperatures and increasing tucked postures during cooler ones, yet there was no clear relationship between the employment of this strategy and the use of forest depth. Possible explanations for the data were explored, including the effect of human interaction. In order to establish more concise patterns for the use of microhabitat selection as a form of behavioral thermoregulation, further research should increase the range of temperatures and the length of the study.

Key Words: lemurs, behavioral thermoregulation, microhabitat climate variation, forest depth, temperature variation

Introduction

Thermoregulation is a key process by which an animal maintains its internal body temperature within a physiological acceptable range despite changing environmental conditions (Schino and Troisi, 1989, Terrien *et al.* 2011, Satinoff 2011). Inability to maintain body temperature within normal range can result in hyper- or hypothermia, or even death. Physiological responses can help control body temperature but they are complex and energetically costly (Nakayama *et al.* 1971, Terrien *et al.* 2011). To compliment these physiological responses, endotherms engage in behavioral thermoregulation or employing behaviors to avoid heat gain in hot ambient temperatures (such as seeking out shade and assuming prone postures on cooler substrates) or to avoid heat loss during cold ones (such as social huddling and increasing ball-like postures; Hanya et al. 2007, Donati *et al.* 2011, and Terrien et al. 2011). Some animals even change the use of their microhabitat as a strategy for adjusting to climatic variation (Hanya 2007, Takemoto 2004, Koshelef and Anderson 2009).

Previous studies have shown that behavioral thermoregulation comprises an important part of a primate's behavioral repertoire (Hill et al. 2004, Takemoto 2004, Hanya *et al.* 2007), but only a handful of studies have focused on these behaviors in lemurs (Morland 1993, Ostner 2002, Donati *et al*. 2011). For lemurs, behavioral thermoregulation strategies may be important to ensure temperature homeostasis in part because they have a lower basal metabolic rate than other primates, and thus a reduced ability to maintain body temperatures physiologically during colder temperatures (Müller 1985). Malagasy lemurs also experience large temperature and humidity fluctuations across the day and across seasons, making behavioral thermoregulation critical for these animals (Harcourt 1990, Sussman 1991, Morland 1993, Ostner 2002, Donati *et al.* 2011). This study aims to broaden our knowledge of behavioral thermoregulation by expanding on the microhabitat selection aspect of behavioral thermoregulation, investigating whether lemurs change the threedimensional use of their habitat (height and depth) in response to climate variation. We will study these behaviors in individuals of *Lemur catta* and *Propithecus coquereli* at the Duke Lemur Center.

Climate Variation within the Forest

A variety of factors affect the microclimate of forests and that these factors vary throughout the forest and across seasons (Christy 1952, Chen *et al.* 1993, Chen *et al.* 1999, Xu *et al.* 1997, Tanja *et al.* 2003). Air temperature is one of the climatic variables that has been shown to differ within a small-scale ecological system (Chen *et al.* 1993, Xu *et al.* 1997, Grimmond *et al.* 2000). A study performed at the Missouri Ozarks showed that air temperature varies significantly even within a single enclosure 80 x 80 m^2 (Xu *et al.* 1997). In their study, placing temperature sensors 40m apart within the same oak and pine wood forested enclosure resulted in a significant temperature difference ranging from 0.7°C to 1.6°C (Xu *et al.* 1997). However, data collection for this study only lasted 15 days and it did not establish any patterns between temperature variation and depth into the forest or forest canopy coverage.

Besides spatial variation, temperature variation was also shown to correlate with different types of forest canopy coverage, identified as forest depths (Chen *et al.* 1993; Ghuman and Lal 2000). One study showed that at the edge of a forest, temperatures experience a greater range of variation, and this range is also dependent on the orientation of the edge (Chen *et al. 1993*). When comparing edge, clear-cut and interior, temperature is lower in the interior of the forest than at the other two locations (Chen *et al.* 1993). This same pattern is also true when comparing a partial clearing to the interior of a humid tropical forest (Ghuman and Lal 1986).

Another climatic factor that has shown small-scale variation is humidity. Studies looking at humidity variation have focused on the differences between humidity at an edge as compared to other parts of the forest. These studies have shown that humidity increases as distance away from the edge increases, a relationship that also correlates with forest coverage (Ghuman and Lal 1986, Matlak 1993, Chen *et al*. 1993, Grimmond *et al.* 2000).

To determine if similar patterns occur in the smaller forested enclosures used by the lemurs in our study, we will first focus on establishing a specific pattern of temperature and humidity variation throughout different depths of the Natural Habitat Enclosures of the Duke Lemur Center.

Microhabitat Selection as a Strategy for Behavioral Thermoregulation

Microhabitat selection has been proposed as a strategy for thermoregulation for a handful of primates (Hanya 2007, Takemoto 2004, Koshelef and Anderson 2009). Previous research, however, has been limited to a few studies mostly focusing on vertical use of the forest. During cold temperatures, Japanese macaques (*Macaca fuscata)* were observed to spend more time in the areas of the microhabitat that offered higher sun exposure, such as open areas in a coniferous forests or in the trees in coastal forests (Hanya 2007). Chimpanzees (*Pan troglodytes)* were also shown to increase the amount of time spent on the ground during hotter or drier environmental conditions (Takemoto 2004, Koshelef and Anderson 2009).

Beside vertical height, another specific factor related to microhabitat selection that has been studied in primates is the use or avoidance of sun exposure as a strategy for behavioral thermoregulation (Hill *et al.* 2004). Several species of primates have been shown to either slow the rate of activity during a hot day when they encounter a shady patch, or to have a preference for sunny places during low ambient temperatures and a preference for shady places during hotter ones (yellow baboons: Stelzner 1988, howling monkeys: Bicca-Marques and Calegaro-Marques 1998, chimpanzees: Koshelef and Anderson 2009). However, research studying other aspects of the microhabitat, such as differential use of forest depth, and research looking at these behaviors in lemurs has been scarce (Morland 1993, Aujard 1998, Ostner 2002, Donati *et al.* 2011).

Other Behavioral Thermoregulatory Strategies

Beside microhabitat selection, there are behavioral thermoregulatory strategies that warm-blooded animals engage in to maintain body temperatures within an ideal range. The thermoneutral zone is the range of temperatures within which metabolic rate remains unchanged, and although this has not been specifically researched for lemurs, it is usually accepted to be between 20°C – 30°C (Daniels 1984, Richard and Nicoll 1987). Behavioral strategies used to remain within this zone may include postural changes that maximize the amount of surface area available for heat exchange during hotter temperatures and minimize surface area to avoid heat loss during colder temperatures. These strategies have been observed in a variety mammals including bats (*Pteropus hypmelanus*) who increase their exposed wing surface and the frequency of wing-fanning behavior, but expose less wing area and decrease fanning behaviors when ambient temperatures are closer to their body temperatures (Ochoa-Acuna and Kunz, T.H. 1999). Similar postural changes in response to temperature variations have also been observed in primates, including in Japanese macaques, howling monkeys, capuchins and chimpanzees (Bicca-Marques and Calegaro-Marques 1998, Hanya 2004, Kosheleff and Anderson 2009, Campos and Fedigan 2009). During warmer temperatures, howling monkeys decrease the use of resting postures and they tend to use heat-dissipating postures, where the body is extended or stretched, more frequently (Bicca-Marques and Calegaro-Marques 1998).

Decreasing activity levels during times of thermoregulatory stress is another behavioral way of conserving energy through thermoregulation. Squirrels (*Spermophilus citellus*) do this by having a bimodal activity pattern with a rest phase at midday when ambient temperatures are highest (Vaczi, *et al.* 2006). Likewise, Japanese macaques change their activity levels by decreasing traveling and feeding times in colder temperatures (Hanya 2004), and chimpanzees and capuchins increase the amount of time spent resting during hotter temperatures (Kosheleff and Anderson 2009, Campos and Fedigan 2009).

Beside using postural changes and adjusting their activity levels, endotherms also use social behavior, such as huddling, as another behavioral thermoregulatory strategy. Huddling maximizes energy saving in an individual by decreasing the amount of body surface area exposed to the cold, and by increasing the ambient temperature surrounding the huddled individuals (Gilbert 2010). Manny mammals including rodents, rabbits, long-tailed macaques, japanese macaques, and lemurs, among others, engage in huddling behaviors during colder temperatures (Alberts 1978, Hull and Hull 1982, Schino and Troisi 1990, Hanya 2007, Donati *et al.* 2011).

Studies focusing on these behaviors in lemurs are scarce, but the studies that have been done have shown that lemurs, like other primates, adjust the amount of resting time, the types of postural activity, microhabitat selection, and the use of social activities in responses to environmental changes (Morland 1993, Ostner 2002, and Donati *et al* 2011). Red fronted lemurs (*Eulemur fulvus rufus)*, redruffed lemurs (*Varicia* variegata), and collared lemurs (*Eulemur collaris* were found to increase the rate of resting behaviors and decrease activity levels, engage in huddling groups more often, and to increase sunning and hunched behaviors during colder temperatures (redfronted lemurs: Ostner 2002, redruffed lemurs: Morland 1993, collared lemurs: Donati *et al.* 2011).

Overall, it is clear that primates, including lemurs, engage in a wide range of behaviors to help maintain their body temperatures stable. Understanding how these strategies are used in combination might give us a better understanding of behavioral thermoregulation in general. For this reason, our study will analyze not only the microhabitat selection aspect of behavioral thermoregulation, but also what other thermoregulatory behaviors lemurs employ, and their relationship to the choice of microhabitat for different climatic variables.

Behavioral Thermoregulation and microhabitat selection in *Lemur catta* and *Propithecus coquereli*

Lemur catta are cat-sized individuals native to Madagascar, ranging throughout southwestern Madagascar in dry and spiny desert forests (Jolly 2003). *L. catta* is the most terrestrial lemur species, and individuals live in large groups of 10 to 20 individuals (Petter 1962, Suther 1999, Jolly 2003, Mittermeier 2006). *Propithecus coquereli* individuals are the biggest of the lemur species (5-7kg). These specialized vertical clingers and leapers have a unique ground locomotion pattern, bouncing around bipedally in sideways kangaroo-like hops. In Madagascar, they range throughout the dry spiny forest and riverine forests of the south and up to the deciduous forests of the west (Mittermeier 2006, Richard 2003). In southwestern Madagascar where the *Lemur catta* are found, temperatures average 34°C - 35°C during the wet season (Novembe-March), with the highest temperatures reaching 48°C, and during the cool dry season, temperatures average between 23°C - 30°C but fall to a low of 3°C at night (Sussman 1991). Similar temperature variation has been observed in the areas inhabited by *Propithecus coquereli* (Sussman 1991). Due to the large daily and seasonal temperature fluctuations that these species are exposed to, behavioral thermoregulation is a very important aspect of these animal's lives.

Overall, based on previous research (Chen *et al.* 1993, Xu *et al.* 1997, Grimmond *et al.* 2000), we expected that during our study period (summer and fall), the deeper into the forest, the cooler the ambient temperatures and the lower the humidity levels would be due to the higher tree coverage keeping sunlight from penetrating. Relating these patterns of temperature and humidity variation to the individuals' behaviors, we expected that lemurs would choose to be at depths within the forest that would bring them closer to their thermoneutral zone. For depth, following our specific prediction for climate variation within the forest, this would mean spending more time at the interior of the forest during hotter temperatures, and at the edge or out during colder temperatures. We also predicted that if these depths were used for behavioral thermoregulation, the animals would also be found engaged in postures and other thermoregulatory behaviors that also help them adjust to the climate. To test these predictions, we focused our study on captive populations of *Lemur cattta* and *Propithecus coquereli* at the Duke Lemur Center and analyzed the correlation between the specific behaviors being performed, the choice of depth in the forest, and the temperatures at which they were being performed

Methods

Part I: Climate Data for the Natural Habitat Enclosures (NHE)

Protocol

We collected temperature and humidity data at different depths in the forest for three natural habitat enclosures at the Duke Lemur Center (DLC; Figures 1 – 4). We placed Extech Rht10 data loggers in each enclosure at five locations:"out", "edge", 5m, 30m, and 60m. "Out" was designated as a location at the entrance of the forested enclosure where there was no tree coverage. The data logger at this location was placed at least one meter away from any nearby fence or man-made structure so that they did not affect the temperature or humidity readings. All other locations were placed in the forest along the path delineated for each enclosure on Images 2-4, usually a path already established by the DLC staff. . "Edge" was considered the point at the start of the path where the tree coverage began. All other depths were measured from this "edge."

Data were collected from late-July through mid-November. The Data Loggers were programmed to collect temperature and humidity on a continuous basis every 30 minutes. Every two weeks, the data were downloaded to a computer to ensure that the devices continued to work properly. If there were any issues during any day of collection, we made a note of it and discarded those points from any future data analysis. In order to download the data, the Data Loggers had to be moved from their locations in the forest, to the main building where the computers were located, and then taken back to the forest after download was completed. For this reason, the first two and the last two data points of every downloaded file were not included in the analysis.

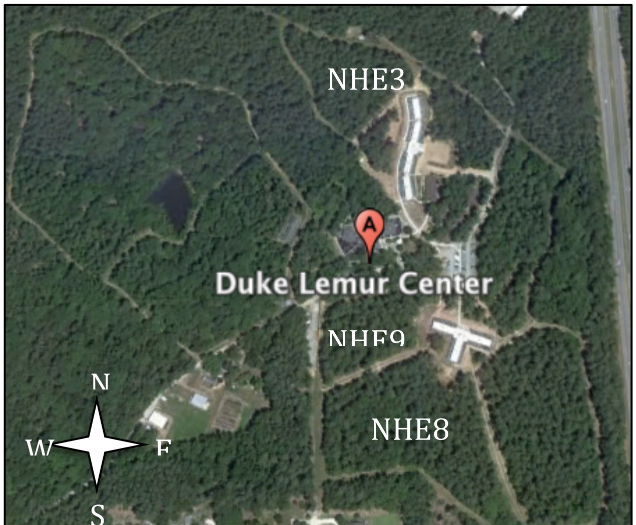

Figure 1: Google Earth image of the three enclosures studied in this study (NHE3, 8, and 9) and their relative locations within the Duke Lemur Center

Figure 2: **NHE 3 Enclosure**. NHE 3 is approximately 10000m^2 in size. The white line indicates the approximate location of the data loggers within the enclosure

Figure 3: **NHE 8 Enclosure**. NHE 8 is about 24300m^2 in size. The white line indicates the approximate location of the data loggers within the enclosure

Figure 4: **NHE 9 Enclosure**. NHE9 is about 14200m^2 in size. The white line indicates the approximate location of the data loggers within the enclosure.

Data Analysis

Temperature and humidity data were summarized for each natural habitat enclosure separately. We scanned for any possible logger errors within the data (such as extreme cold temperatures or zero humidity) and discarded these data points from future analysis. For each depth category (out, edge, 5m, 30m, 60m), we then found the average temperature and humidity, as well as the ranges for the entire time of data collection. To control for the change in leaf coverage between summer and fall, we also separated our data by month, and found the averages and ranges at each depth category for each month observed.

Part II: Behavioral Data Collection

Subjects and Housing

Our subjects consisted of a total of 22 individuals: 13 individuals of *Lemur catta,* five males and eight females, and nine individuals of *Propithecus coquereli*, six males and three females (Table 1). The ages of our adult subjects ranged from 1.0 to 24.2 years old, with only two *P. coquereli* infants outside of this range (Pontius Pilate and Ferdinand, both 3 months old at the start of the study). Individuals were identified using collars, shavings, or other distinguishing characteristics.

Table 1: **Individuals Observed** Individual's name, sex, age, location at the Duke Lemur Center and species are given. The ages here represent the ages at the start of the study.

Enclosure	Individual's Name	# Observations	Sex	Age	Species
NHE 3	Aristides	15	M	20.1	*Lemur catta*
	Sosiphanes	14	F	16.1	
	Lilah	10	F	8.1	
	Jovian	15	M	19.1	*Propithecus coquereli*
	Conrad	14	M	4.3	
	Ferdinand	---	M	0.3	
	Pia	12	F	14.2	
NHE 6	Aracus	9	M	22.0	*Lemur catta*
	Johan	11	M	3.0	
	Rolfe	12	M	2.0	
	Shroeder	10	F	21.1	
	Brigitta	9	F	2.0	
	Liesl	7	F	4.8	
	Gretl	11	F	1.0	
NHE 8	Fritz	7	M	11.0	*Lemur catta*
	Dory	9	F	24.2	
	Alena	9	F	8.1	
NHE 9	Julian	12	M	20.2	*Propithecus coquereli*
	Martinianus	16	M	5.3	
	Pontius Pilate	---	M	0.3	
	Drusilla	12	F	20.1	
	Arcadia	13	F	2.3	

Most individuals were housed in the same enclosures used to analyze the climate data in this study (NHE3, 8, and 9), but seven of the *Lemur catta* were housed in one extra enclosure, NHE6 (Table 1). All subjects had access to a series of indoor cages, outdoor cages, and the NHE enclosures. The indoor cages are 3.0m by 2.3m by 2.1m in size and each group had access to the same number of cages as at least half the size of their group. The indoor cages were in a climate controlled building with temperature kept constant at 22°C. The indoor cages were also connected to the outdoor cages that ranged from small (3.0m by 2.1m by 4.3m) to large (3.0m 3.5m by 4.3m), and which were exposed to natural climatic changes. The individuals had access to the same number of outdoor cages as indoor cages. Both indoor and outdoor cages are surrounded by chain link fence and are equipped with enrichment objects and structures. All of the outdoor cages also connect to the NHE enclosures that range between 1 hectare and 2.7 hectares in size. These enclosures consist mature secondary semi-deciduous forests, consisting mainly of pine and hardwood trees, with the highest trees reaching 30m in height, and they are surrounded by a 1.8m high chain link. Electrified wires run across the tops of the fence and deliver a small electric shock on contact to keep the animals contained within the enclosures.

For the duration of our study, all individuals were semi-free ranging, having unlimited access to the indoor cages, the outdoor cages and the forested enclosures. This access was restricted when daytime temperatures dropped below 4°C or when overnight temperatures were predicted to be below 4°C within 48 hours, in which case the animals were locked in the indoor cages. Observations took place in the outdoor enclosures and the NHE enclosures where the animals were exposed to natural climatic variation. If an individual travelled to the indoor cages for part of an observation that had started elsewhere, data collection continued, but any behavior observed during this time was excluded from calculations because of the controlled nature of the climate in this location.

Individuals had unlimited access to foods naturally found in the forest: leaves, flowers, twigs, etc. In addition, subjects received daily supplemental food from the DLC staff consisting of nutritious chow, some fruit and veggies, and sometimes some fresh browse. The feeding times usually took place sometime between 10am – 11:30am, and if browse was supplied, this usually happened between 2pm and 3pm. The animals were fed at feeding stations found within the NHE enclosures or in their cages when they were not in the NHEs. Any food left over at the feeding stations after feeding time remained accessible to the animals at this location for the rest of the day.

Protocol

Our study took place from late-July to mid-November. We collected a total of 226 observations (Table 1). Data were collected using Psion Workabout Pro event recorders and programmed with The Observer Software (version 11; Noldus 2013). We used focal animal sampling with focal durations of 20 minutes each (for a total of 5200 minutes of observation). Behaviors regarding the activity level (i.e. locomotion, sitting, eating or drinking, etc.) were recorded on a continuous basis (Appendix I). For sedentary behaviors, such as sitting or clinging, postural information was also recorded (i.e. extended limbs vs tucked while sitting, open vs. closed while clinging; Appendix I).

In order to test whether lemurs change the way they use the forest in response to climate variation, we also recorded information regarding the individual's depth within the forest on a continuous basis for each behavior observed (Table 2). Depth measurements within the enclosures where the animals were housed and depth categories were established prior to the start of behavioral observations. Depth markers were placed at 5m, 30m, and 60m into the enclosure from a given path (Figure 2-4). Depth for each particular behavior was systematically assigned by the observer using the markers as a guide.

Table 2: **Depth Categories** Definition of each depth category, determined before the start of behavioral observations.

Depth Category	**Definition**
Out	Sections of the forested enclosure with no tree coverage, indoor cages, outdoor cages, and fenced walkway to forested enclosure.
Edge	From any start of tree coverage along the forest perimeter to 5m into the forest tree coverage.
5m	From 5m into the forest to 30 meters into the forest
30m	30m into the forest to 50m
60m	50m into the forest to forest center (between 60m and 80m from edge)

At the end of each 20-minute focal, temperature, humidity, wind speed, and heat index were recorded using a Kestral 3000 pocket weather meter. The meter was placed at arm's length from the body and once the reading settled on a point for three seconds, the information was recorded. Information regarding sun levels (clear skies, scattered clouds or overcast) and presence or absence of rain was also recorded at the end of each observation.

Data Analysis

Data were summarized per individual first and then across members of the same species per enclosure. Since infants spent most of their time clinging to their mothers and not making their own decisions about location in the forest, we excluded data for the two infants from our analysis. Percentages of time spent at each depth category for a specific temperature category was calculated. Temperatures were categorized into bins of five degrees each starting at 10.1°C and ending at 35.0°C. To further assess whether use of forest depth was a behavioral thermoregulatory response, we analyzed the sun exposure level associated with the use of the particular depths at a given temperature category. We also calculated the percentage of time spent in different postures while seated for different temperatures and depths.

To see if the level of sun exposure affected the lemurs' use of forest depth during different temperatures we calculated what percent of the time during the different sun exposure levels were spent at each depth for a given temperature category. For this analysis we combined all habitat enclosures to reduce the effects of small sample size. For the same reason, we combined clear and scattered days together and contrasted it to overcast days

Results

Part I: Climate Data for the Natural Habitat Enclosures (NHE)

We analyzed the temperature and humidity data collected from mid-July to mid-November for general trends across depth in the forest. Since the data loggers were placed within each enclosure along paths that differed on the orientation of the sun, we analyzed the data for each enclosure separately.

A: Temperature Variation at Different Depths

Natural Habitat Enclosure 3 (Refer to Figures 1-2)

The temperatures for all depths in NHE 3 ranged from a minimum temperature of -5.2°C to a maximum temperature of 52.1°C across the study period, with “5m” having the most variation, ranging from a minimum of -4.7°C to a maximum of 49.7°C, and 60m having the least variation with temperatures ranging from -4.9°C to 34.5°C.

When comparing the average temperature for all data (all months combined) across the different depth categories (“out”, “edge”, 5m, 30m, and 60m), there was no clear pattern observed. “Edge” had the highest average temperature at 23.0°C and 30m had the lowest average temperature at 17.6°C.

When comparing the temperature variation across the different depth categories per month, temperatures tended to decrease as depth into the forest increased (Figure 5). Although this pattern was not always constant for all the different depths, “out” during all months had an average temperature that was higher than 60m. The difference in temperature between “out” and 60m was largest during July (3.7°C difference) and this difference decreased as the temperatures cooled, with less than a one-degree difference in November.

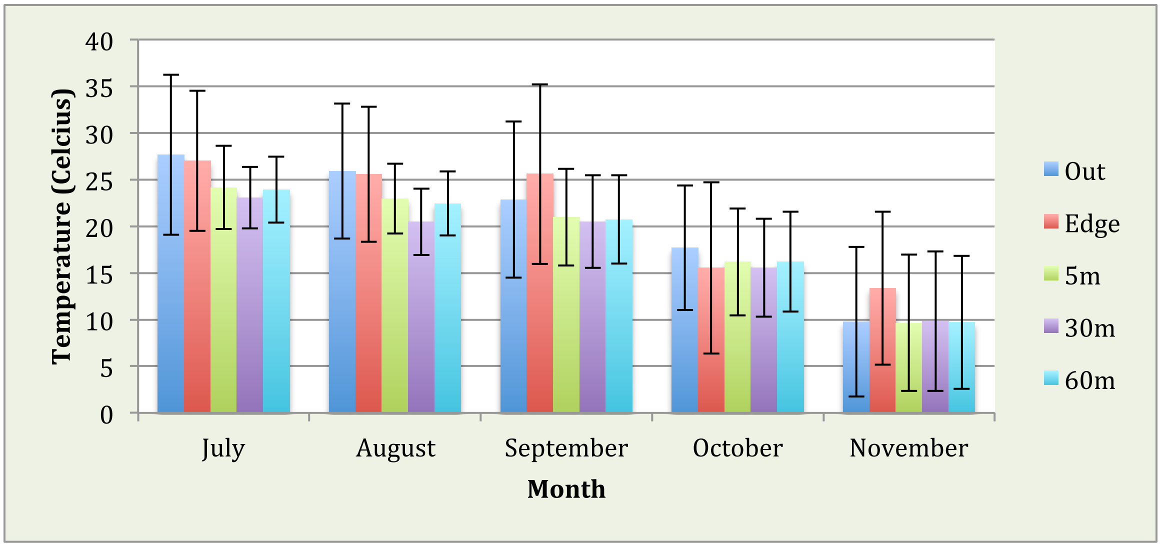

Figure 5: NHE 3 Average temperature variation for different depths analyzed by month. All bars represent average temperature for each depth category during the specific month. The error bars indicate standard deviation from the average. Note that data collection ended on November 15th so there is less data for this month, and thus, greater standard deviation.

Natural Habitat Enclosure 8 (Figure 1, 3)

The temperature from all data collected in NHE 8 ranged from a minimum of -5.1°C to a maximum of 46.5°C, a few degrees lower than the maximum observed in NHE 3. In this enclosure, "edge" had the most variation in temperature, having temperatures that ranged from -5.1°C to 45.6°C, while 60m still had the least variation, with a minimum of -3.4°C and a maximum of 33.0°C.

When comparing the average temperatures across the different depth categories for all months combined for NHE 8, there is no clear pattern to the variation. All of the depths had averages within one degree Celsius of each other, with "out" experiencing the highest average temperature of all the depths at an average temperature of 19.1°C, and 60m experiencing the lowest average temperature at 18.3°C.

When comparing the temperature variation across the different depth categories per month, the temperatures tend to decrease with depth into the forest during the summer months (July and August), but stabilized or slightly increased with depth for the fall months (September, October and November; Figure 6). This pattern is specially strong when comparing “out” to 60m. During August and July, “out” was approximately two degrees warmer than 60m. During September, “out” was approximately the same temperature as 60m, and during October and November, “out” was approximately one degree cooler than 60m.

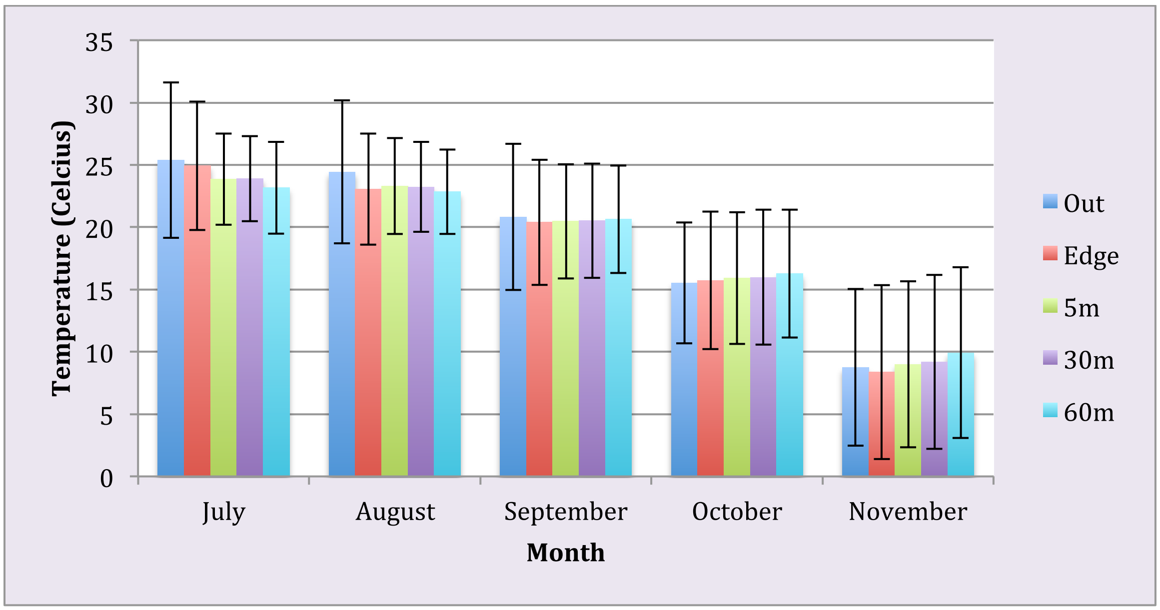

Figure 6: NHE 8 Average temperature variation for different depths analyzed by month. All bars represent average temperature for each depth category during the specific month. The error bars indicate standard deviation from the average. Note that data collection ended on November 15th so there is less data for this month, and thus, greater standard deviation.

<u>Natural Habitat Enclosure 9</u> (Figure 1, 4)

The temperature from all data collected in NHE 9 ranged from a minimum of -5.5°C to a maximum of 54.0°C. In this enclosure, “out” had the most variation in temperature, having temperatures that ranged from -4.9°C to 54.0°C, while as in NHE 3 and NHE 8, 60m also had the least variation, with a minimum of -4.4°C and a maximum of 40.4°C.

Table 4: Comparison of Temperature and Depth relationships across the different enclosures

	Greatest Temperature Variation	Least Temperature Variation	Highest Overall Average Temp	Lowest Overall Average Temp	Overall Trend of Temperature Variation
NHE 3	5m	60m	Edge	30m	Decrease with depth
NHE 8	Edge	60m	Out	60m	Decrease with depth in summer and increase in fall
NHE 9	Out	60m	Out	60m	Decrease with depth

When comparing the average temperatures across the different depth categories for all months for NHE 9, temperatures tend to decrease as we go deeper into the forest, similar to in NHE 3 and in NHE 8 during the summer (Table 4). Although all of the temperatures were within two degree Celsius of each other, there was a decline in temperature from the highest at "out" (20.8°C) to the lowest at 60m (18.8°C).

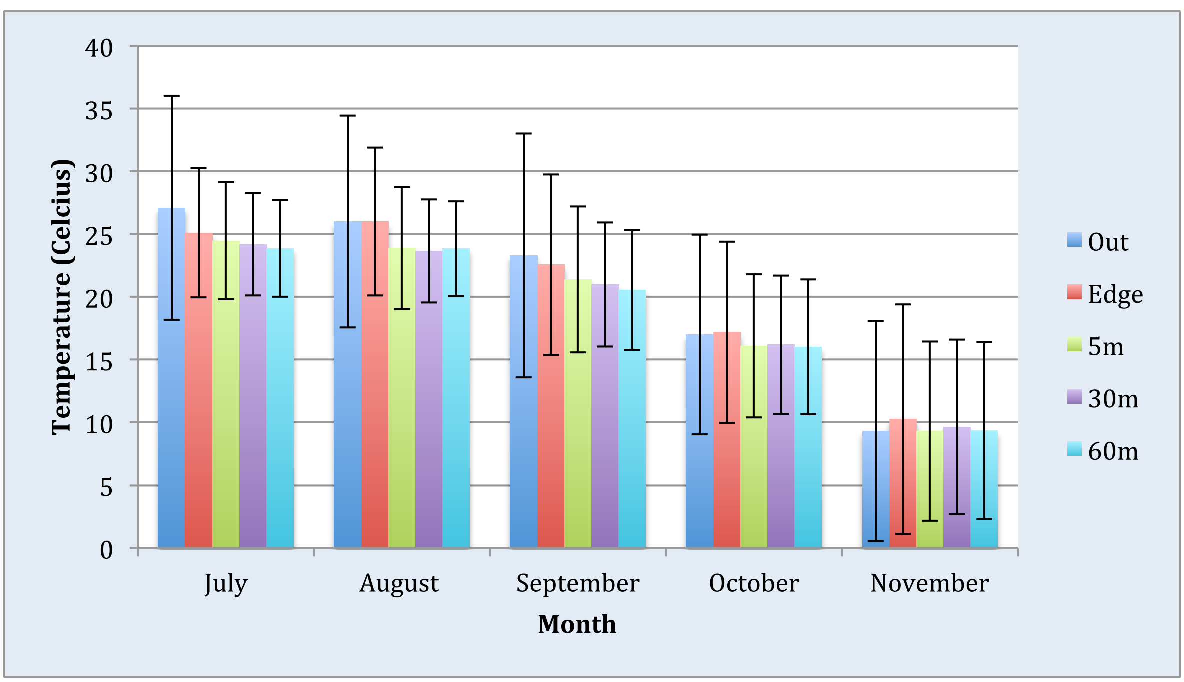

Figure 7: NHE 9 Average temperature variation for different depths analyzed by month. All bars represent average temperature for each depth category during the specific month. The error bars indicate standard deviation from the average. Note that data collection ended on November 15th so there is less data for this month, and thus, greater standard deviation.

When comparing the temperature variation across the different depth categories per month, temperatures tended to decrease as we went deeper into the forest. In all months except November, "out" had an average temperature that was higher than that of 60m, with this difference in temperature being biggest in July (3. 2°C difference) and decreasing each month (Figure 7). In November, the average temperatures from "out" and 60m did not differ, both being at 9.3°C.

B. Humidity Variation at Different Depths

Natural Habitat Enclosure 3

The percent humidity levels in NHE 3 ranged from a minimum of 1.4% to 100%. All locations reached 100% humidity as their maximum. In this enclosure, "edge" had the most variation in humidity, ranging from 1.4% humidity to 100%, and 60m had the least variation, with a minimum of 25.2% and a maximum of 100%.

When comparing the average humidity level across the different depth categories for all months for NHE 3, with the exception of "out", average humidity tended to increase as depth into the forest increased. The average percent humidity at "out" was 84.8%, at "edge" it dropped to 75.8%, and then it increased from "edge" to 60m, which had an average percent humidity of 85.5%.

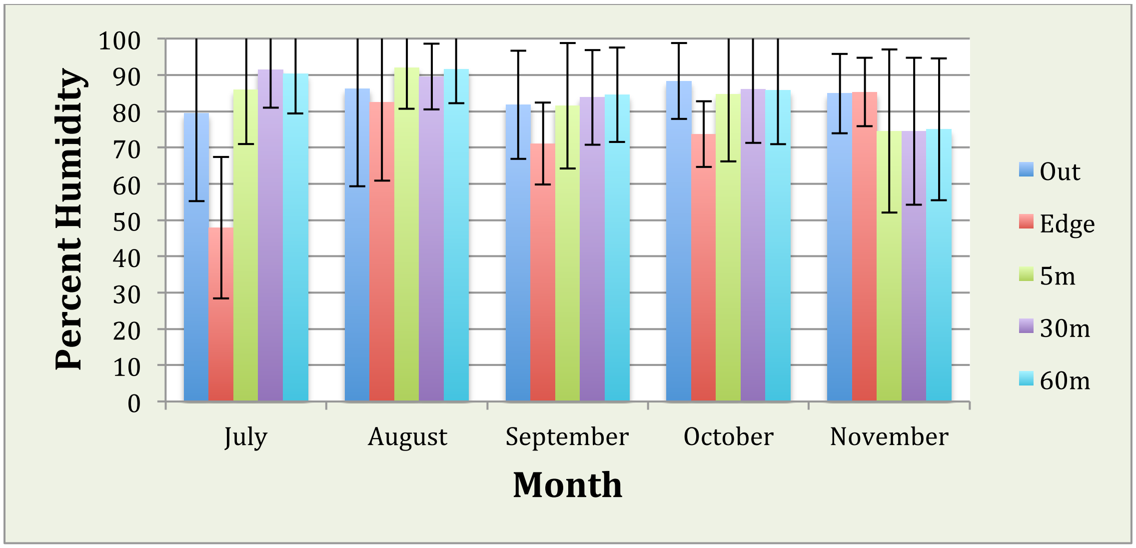

Figure 8: NHE 3 Average percent humidity variation for different depths analyzed by month. All bars represent average percent humidity for each depth category during the specific month. The error bars indicate standard deviation from the average.

When comparing the average percent humidity variation across the different depth categories per month, with the exception of "edge" on all locations, average percent humidity tended to increase as we went deeper into the forest during the summer months (July, August and September) and tended to decrease deeper into the forest during the fall months (October and November; Figure 8). This trend holds true especially when comparing "out" to 60m.

Natural Habitat Enclosure 8

The percent humidity levels in NHE 8 ranged from a minimum of 2.1% to 100%. In this enclosure, "out" had the most variation in humidity, ranging from 2.1% humidity to 100%, and 5m had the least variation, with a minimum of 34.8% and a maximum of 99.6%.

When comparing the average humidity level across the different depth categories for all months for NHE 8, average humidity tended to increase as depth into the forest increased, with "out" having an average percent humidity of 84.7% and 60m having an average percent humidity of 87.4%.

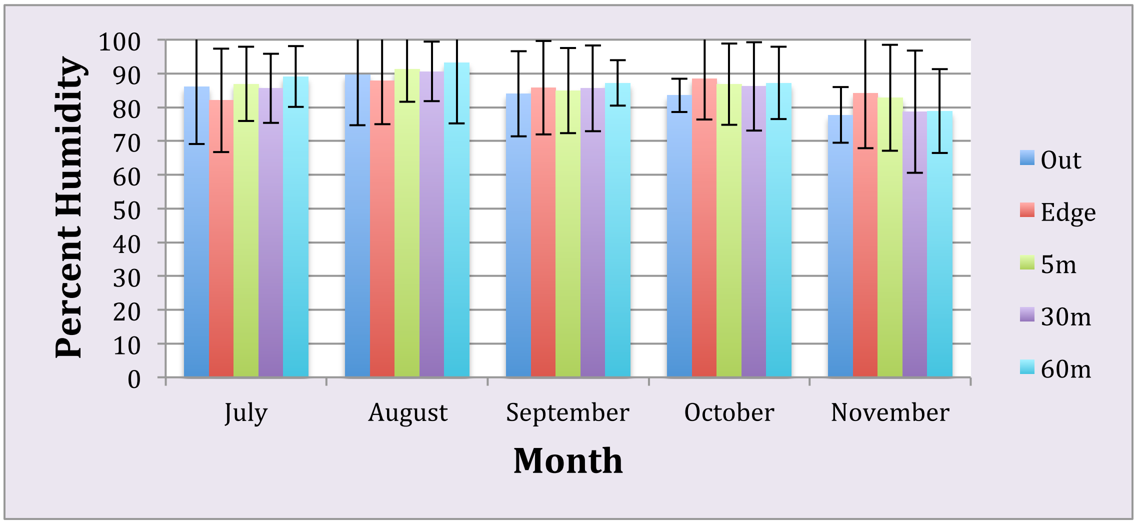

Figure 9: NHE 8 Average percent humidity variation for different depths analyzed by month. All bars represent average percent humidity for each depth category during the specific month. The error bars indicate standard deviation from the average.

When comparing the average percent humidity variation across the different depth categories per month, there is no definite pattern (Figure 9). However, average percent humidity at all months was lower at "out" than it was at 60m by at least 1%.

Natural Habitat Enclosure 9

The percent humidity levels in NHE 9 ranged from a minimum of 10.1% to 99.6%. In this enclosure, "out" had the most variation in humidity, ranging from 12.7% humidity to 99.6%, and 30m had the least variation, with a minimum of 25.2% and a maximum of 99.2%.

When comparing the average humidity level across the different depth categories for all months for NHE 9, there is no clear pattern in the data. "Out" had a higher humidity than "edge", and 60m had a higher humidity than 30m. However, "out" did have a lower average percent humidity than 60m, like in enclosures NHE 3 and 8 (Table 5).

Table 5: Comparison of Percent Humidity and Depth relationships across the different enclosures

	Greatest Percent Humidity Variation	Least Percent Humidity Variation	Highest Overall Average Percent Humidity	Lowest Overall Average Percent Humidity	Overall Trend of Humidity Variation
NHE 3	Edge	60m	60m	Edge	Increase with depth in summer and decrease with depth in fall
NHE 8	Out	5m	60m	Out	No clear pattern, out always lower than 60m
NHE 9	Out	30m	30m	Edge	Increase with depth in summer and decrease with depth in fall

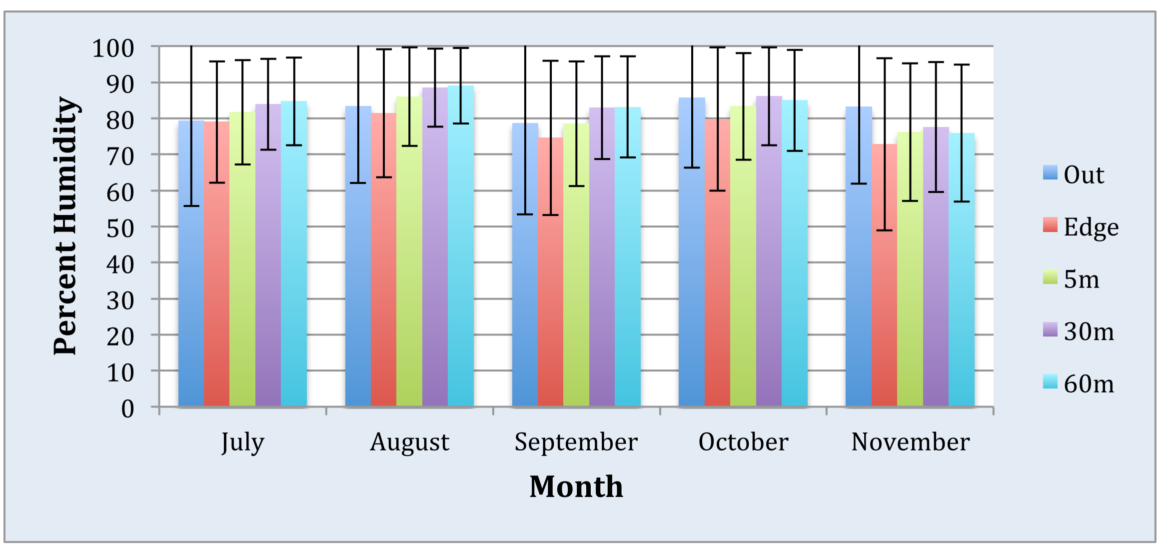

Figure 10: NHE 9 Average percent humidity variation for different depths analyzed by month. All bars represent average percent humidity for each depth category during the specific month. The error bars indicate standard deviation from the average.

When comparing the average percent humidity variation across the different depth categories per month, average humidity tended to increase as depth into the forest increased during the summer months (July, August, and September) but the pattern disappears during fall (October and November; Figure 10). A comparison of out to 60m showed a more consistent pattern, with humidity increasing with depth into the forest during summer, and decreasing with depth into the forest in fall.

Part II: Behavioral Analysis

To examine how the lemurs change the use of the forest in response to temperature variation, we analyzed what percent of their time was spent at a given depth within a given temperature category. Each enclosure faced the sun at a different orientation and the trends in temperature analyzed in the first part of this study slightly differed for each enclosure, thus we analyzed the data for each enclosure separately.

A. Changes in Use of Forest Depth in Response to Temperature Variation

NHE 3:

Natural Habitat Enclosure 3 is the only enclosure in this study that contained both species of lemurs (3 individuals of *Propithecus coquereli* and 3 of *Lemur catta)*. For this reason, we first analyzed the data for each species separately.

For *Propithecus coquereli,* at all temperature categories (from 15.1°C - 35.0°C), individuals spent the majority of their time at the edge (approximately 50%

of the time at each temperature category), and were rarely observed at 30m or 60m (less than 10% of the time for any given temperature category; Appendix II).

For *Lemur catta*, irrespective of temperature, individuals spent the majority of the time at edge or 5m. In this case, percent time spent at 30m did increase as temperatures got hotter, with 44.4% of the time being spent at this depth in temperatures between 30.1°C - 35.0°C, yet individuals also spent the same amount of time at edge within this temperature category (Appendix III). Furthermore, individuals spent less than 2% of their time at 60m for any given temperature category. It is important to note that sample size was small (10 or less) for temperatures below 20.0°C and above 30.0°C (the thermoneutral zone).

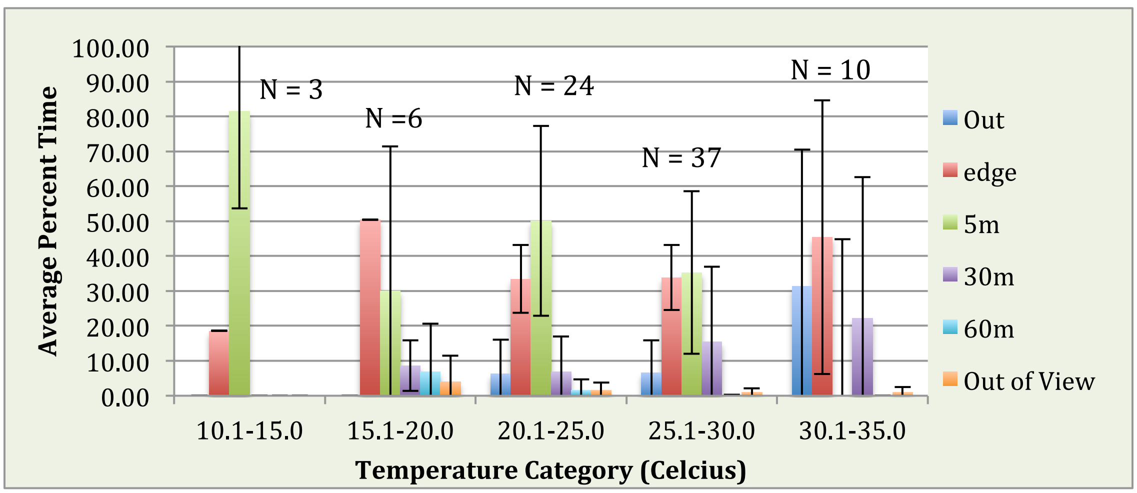

Figure 11: Average percent time within each temperature category spent at a given depth by all individuals of NHE 3. The bars represent what percent of the total observed time at the temperature category individuals spent within a given depth. N is the total number of 20 minute focals that were collected at the given temperature category across the 6 individuals. The bars indicate the standard deviation from the average.

Because the results for *Propithecus coquereli* and *Lemur catta* separately did not show major species differences, we combined the data for the entire enclosure to increase sample size and minimize the effect of individual preferences on the average percent time they spent at each depth. The analysis across all individuals showed that individuals preferred spending the majority of the time during any given temperature at edge or 5m, with 30m being used more often during the hotter temperatures (25.1°C - 35.0°C) but never at a higher percentage than edge (Figure 11). It is important to note that in this enclosure the feeding station is found at edge, and individuals were often seen moving to this location in anticipation of being fed. Furthermore, 60m was rarely used, with 15.1°C - 20.0°C being the only category where the average percentage of time spent at this depth exceeded 2% (at 4.6%). It is also interesting to note that the use of out increased as temperatures got hotter, with 31.3% of the time being spent at this depth in temperatures between 30.1°C to 35.0°C. Out of the forest in this enclosure included a wooden stairwell as well as the outdoor cages, which had partial roof covering.

NHE 6

Natural Habitat Enclosure 6 contained seven individuals of *Lemur catta*. When analyzing the average percent time within a given temperature category that the individuals spent at each depth, we found that individuals spent the majority of the time either at out or edge for all temperatures (Figure 12). In this enclosure, the feeding station was also found on the edge of the forest, and individuals were observed to stay near this location at times before and after being fed. The use of 60m increased as temperatures got hotter with 15.7% of the time being spent at this depth within 30.1°C – 35.0°C temperatures, but the percent of time spent at this depth was always less than that at either edge or out by at least 15%. It is important to note that there are no observations for these individuals in the colder temperatures (below 20.0°C) because during these temperatures, they were usually found in the climate controlled indoor cages.

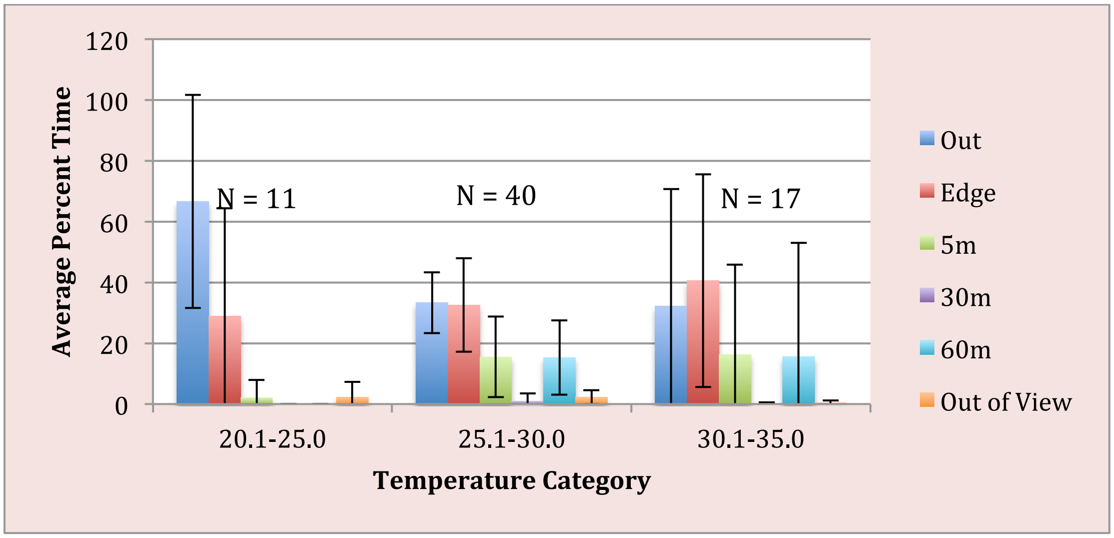

Figure 12: Average percent time within each temperature category spent at a given depth by all individuals of NHE 6. The bars represent what percent of the total observed time at the temperature category individuals spent within a given depth. N is the total number of 20 minute focals that were collected at the given temperature category across the 7 individuals. The bars indicate the standard deviation from the average.

NHE 8

In Natural Habitat Enclosure 8, we observed three individuals of *Lemur catta.* In this enclosure, the feeding station was located at 60m, and this enclosure was composed of a higher density of evergreen forest than the other enclosures. There are no observations at temperatures higher than 30.0°C. Individuals in this enclosure were often difficult to find, especially during the hotter days when they presumably went deep into the forest.

When analyzing the average percent time that the individuals spent at each depth within the given temperature categories, we found that they spent the majority of the time at either edge or 5m regardless of the temperature (Figure 13). In this enclosure The use of 60m increased as temperatures got hotter, with 27.8%

of the time being spent at this depth for temperatures between 25.1°C - 30.0°C, but this percentage was never higher than that of edge or 5m for a given temperature category (Figure 9).

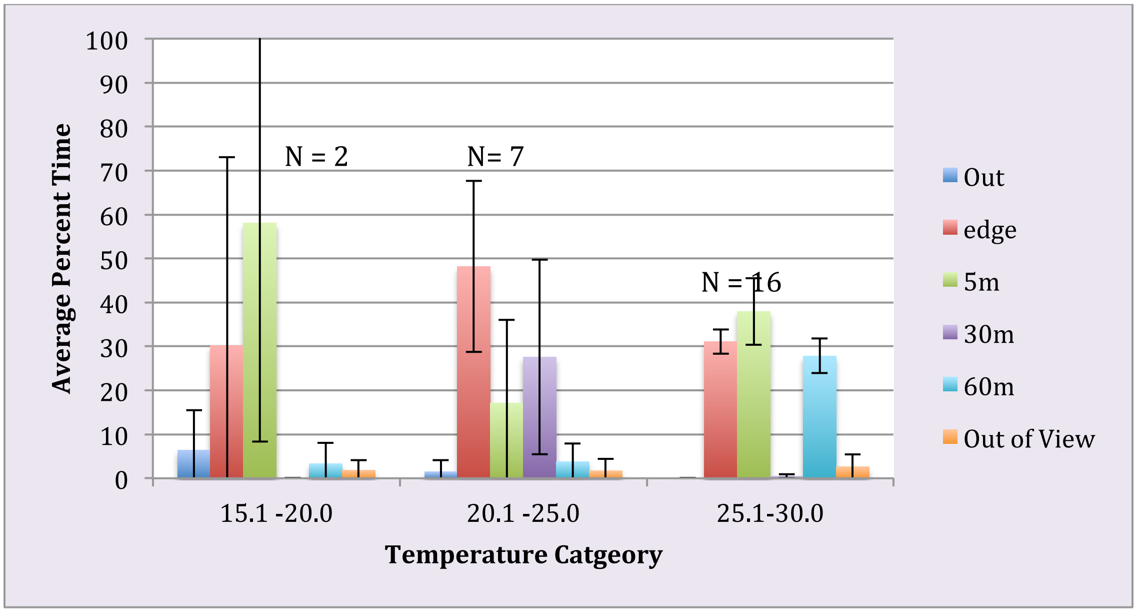

Figure 13: Average percent time within each temperature category spent at a given depth by all individuals of NHE 8. The bars represent what percent of the total observed time at the temperature category individuals spent within a given depth. N is the total number of 20 minute focals that were collected at the given temperature category across the 3 individuals. The bars indicate the standard deviation from the average.

NHE 9

Natural Habitat Enclosure 9 contained four individuals of *Propithecus coquereli.* In this enclosure, the feeding station was found at 30m. Out in this enclosure included a covered bridge as well as the outdoor cages containing partial roof coverage.

When analyzing the average percent time that the individuals spent at each depth within the given temperature categories, we find that individuals spent the majority of the time at either out or 5m regardless of the temperature (Figure 14). The use of 30m and 60m was less than 11% at all temperature categories.

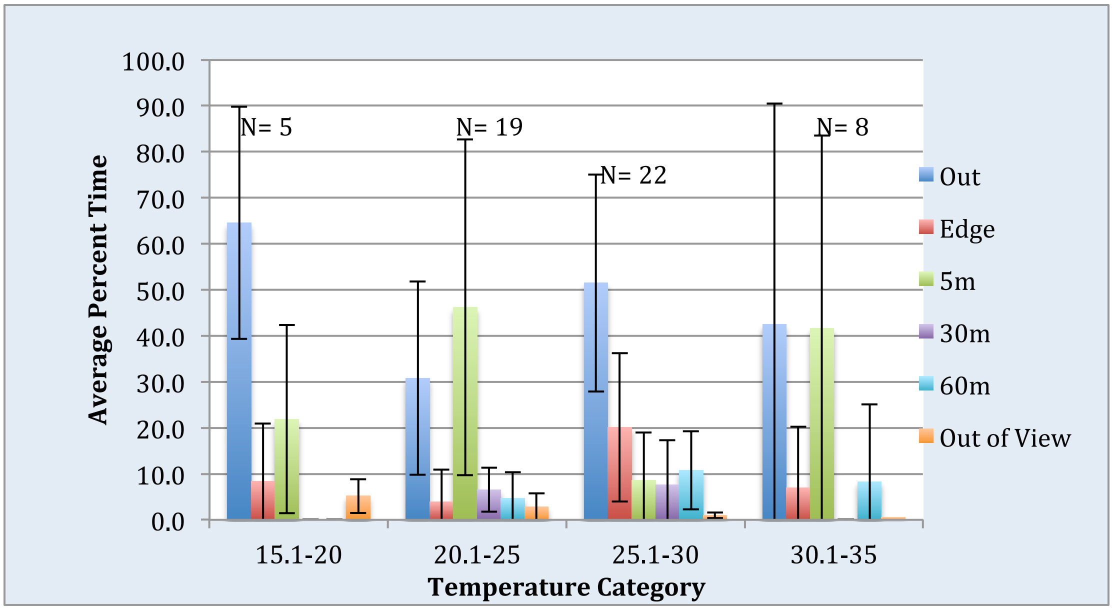

Figure 14: Average percent time within each temperature category spent at a given depth by all individuals of NHE 9. The bars represent what percent of the total observed time at the temperature category individuals spent within a given depth. N is the total number of 20 minute focals that were collected at the given temperature category across the 4 individuals. The bars indicate the standard deviation from the average.

B. Effect of Sun Exposure on use of forest depth for various temperatures

We analyzed how the level of sunlight affected the use of forest depth for different temperature categories. From our 226 observations we discarded 2 observations because they did not have a recorded sun exposure level. Of the remaining 224 observations, 99 occurred during overcast days, 93 during scattered days, and 33 during clear, sunny days.

During sunny and scattered days combined, individuals spent the majority of their time at the edge of the forest during colder temperatures (15.1°C -20.0°C), with no time spent at neither 30m nor 60m at this temperature (Figure 15). For temperatures between 20.1°C and 30.0°C, individuals spent most of their time at edge and 5m. It is interesting to note that the use of out increased continuously as temperatures got hotter, with the majority of the time being spent at this depth during the hottest temperatures (30.1°C to 35.0°C). The use of 30m and 60m also increased slightly during the hotter temperatures, but individuals spent the least amount of time at these depths at all temperatures.

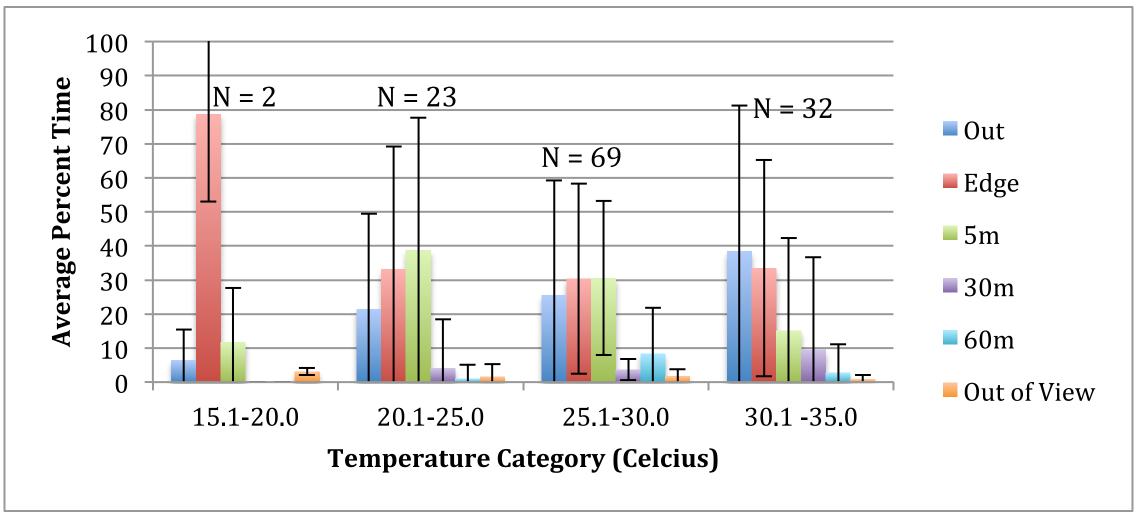

Figure 15: Average Percent Time during clear and scattered days spent at different depths in the forest for each temperature category. The bars represent what percent of the of observed time for clear and scattered days individuals spent within a given depth during a specific temperature category. N is the total number of 20 minute focals that were collected at the given temperature category across all 22 individuals. The bars indicate the standard deviation from the average.

During overcast days, individuals spent the majority of their time at 5m during the cooler temperatures (10.1°C to 20.0°C; Figure 16). As in the clear and scattered days, the use of out during overcast days increases continuously as temperatures increase, with individuals spending the majority of their time at this depth during the hottest temperatures (25.1°C to 35.0°C). It is important to note that the use of 60m was higher for overcast days than for clear and scattered days for all temperature categories. The use of 60m was highest during the hottest temperatures (30.1°C to 35.0°C).

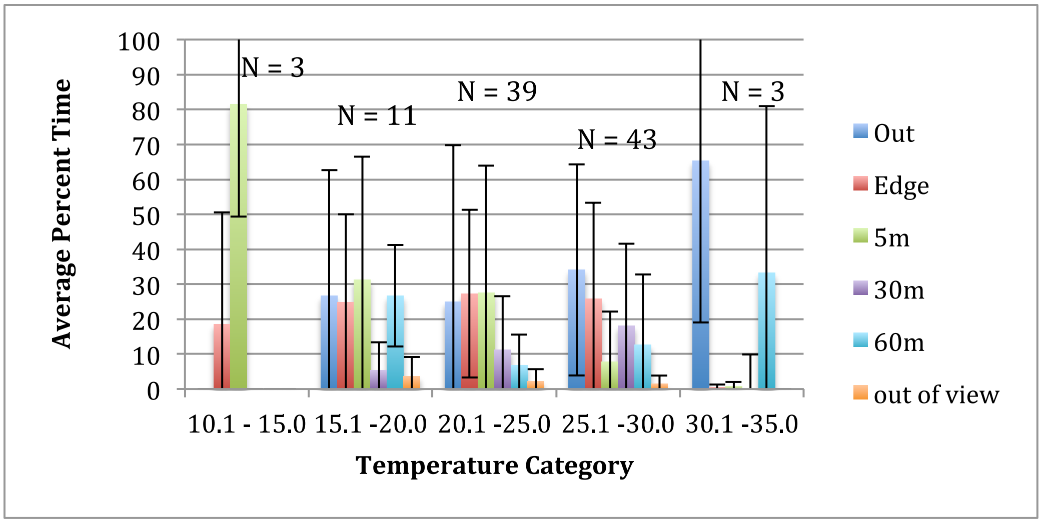

Figure 16: Average Percent Time during overcast days spent at different depths in the forest for each temperature category. The bars represent what percent of the of observed time for clear and scattered days individuals spent within a given depth during a specific temperature category. N is the total number of 20 minute focals that were collected at the given temperature category across all 22 individuals. The bars indicate the standard deviation from the average.

C. Postural Changes in Correlation with Forest Depth for various temperatures

Subjects spent 47% of total observation time seated, with postures divided into energy conserving (tuck, tail wrap, and sunning), energy dissipating (extended), and neutral sit (Appendix I). A general analysis of how individuals change their seated postures in response to temperature variation irrespective of depth in the forest found that neutral sit happened throughout all temperatures, with higher use during colder temperatures than warmer temperatures (55% of the time at 10.1°C - 15.0°C, while 29% of the time at 30.1°C – 35.0°C). Tail-wrap alone was rarely observed (less than 3% of the time at all temperatures) as the majority of the time that individuals would tail wrap they would further their postural sit into a tuck by also tucking their heads into their bodies. Up-sunning was also rarely observed, with the majority of the occurrences happening at temperatures below 25.0°C, and usually in the mornings. For this reason, further analysis will focus on the comparison between tucked and extended.

The amount of time spent in an extended posture increased as temperatures increased while the amount of time spent in a tucked posture decreased (Figure 17). For temperatures between 10.1°C and 15.0°C, individuals were never seen in an extended posture while 47% of the time they were in a tucked posture. For temperatures between 30.1°C – 35.0°C, 66% of the time was spent in an extended posture and less than 3% in a tucked posture.

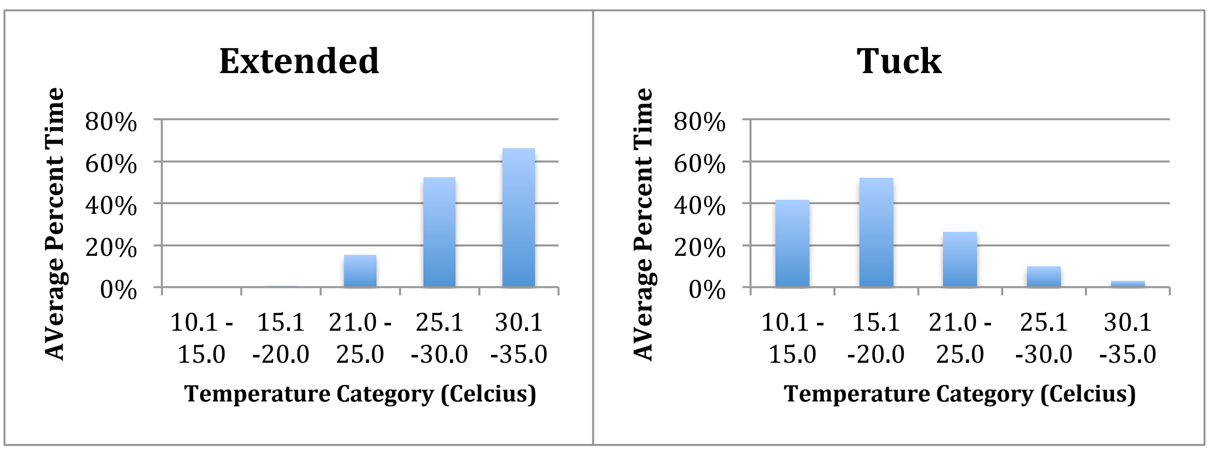

Figure 17: Comparison of Extended Sit vs Tucked Sit for different temperatures. The bars indicate the percent of time while seated spent assuming each posture.

When comparing how the use of extended sit and tucked sit correlated to the use of forest depth we found that for both depths, extended sit occurred more often in hotter temperatures (above 25.0°C) while tucked sit occurred more often in cooler temperatures (below 25°C degrees; Figure 18). There was no clear difference between the amount of time spent in extended sit at edge versus 60m. When looking at tucked postures, for all temperatures except 20.1°C – 25.0°C, individuals spent more time tucked at the edge than at 60m. For the temperature range of 20.1°C - 25.0°C, the pattern reverses and individuals spent more time tucked at 60m than at edge.

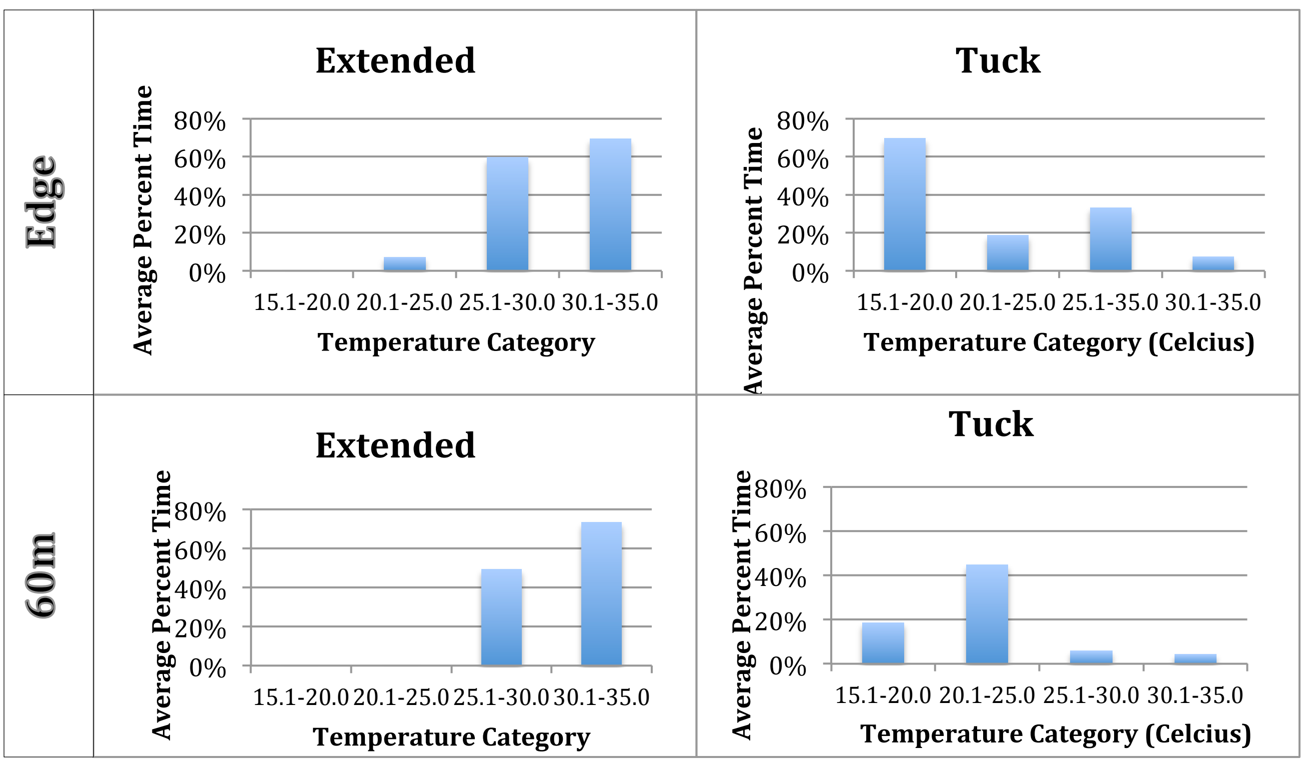

Figure 18: Correlation between Extended Sit and Tucked Sit and forest depth for different temperatures. The bars indicate the percent of time while seated that individuals spent assuming each posture.

Discussion

Climate Variation within the Forested Enclosure

When analyzing how the temperature varied as depth into the forest increased for the different enclosures, we found that generally, temperatures got cooler deeper into the forest, especially during the summer months. This pattern was especially true if we compared the average temperature of the "out" category (out of the forest) to the average temperature of 60m within the forest, by month, which resulted in a difference as high as 3.7°C for one of the enclosures. However, the strength of this pattern decreased in the fall months for which the difference between out and the interior of the forest (the 60m category) was less than 1°C for the enclosures with more deciduous trees (NHE 3 and NHE 9) and which reversed for the enclosure with few deciduous trees (NHE 8) with the outside areas of the enclosures being cooler than the interior of the forest by almost 1°C. Our results are consistent with pervious studies comparing temperatures of the interior of the forest to partial clearings or to edge and clear-cut which also found that the interior of the forest had lower temperatures than other locations (Ghuman and Lal 1986, Chen *et al. 1993*). The interior of the forest (the 60m category) in our study also showed the least variation in temperature for all enclosures, exhibiting the least difference between the minimum and maximum temperatures observed.

For humidity variation, we found that overall, humidity tended to increase as depth into the forest increased during the summer months, especially when comparing out of the forest to the 60m depth. During the fall months, the enclosure with few deciduous trees (NHE 8) continued to have humidity increase with depth, but the difference between out and 60m was smaller, and for the enclosures with deciduous trees, humidity started to decrease with depth. These relationships are consistent with previous studies that have found that humidity increases as depth into the forest increase or as forest coverage increases (Ghuman and Lal 1986, Matlak 1993, Chen *et al*. 1993, Grimmond *et al.* 2000).

Lemurs Use of the Microhabitat as a form of Behavioral Thermoregulation

If the animals use their microhabitat as a behavioral thermoregulatory strategy, then we expected them to adjust their location, in particular depth in the forest, as temperature varies. Specifically, we expected that during hot days individuals would spend their time in areas of the forest that are cooler and during cold days, they would be in areas of the forest that are warmer in order to bring their body temperature closer to their thermoneutral zone. Given the results of our analysis of temperature variation within our enclosures, we thus hypothesized that individuals would spend more of their time at 60m during the hottest days, while during colder times, they would spend the majority of their time in areas that are warmer and receive more sun such as edge or out.

Contrary to our predictions we found that regardless of temperature, individuals in all enclosures tended to have a preference for out and edge over other depths, and that they rarely spent time at 60m. For most of the enclosures, individuals did spend more time deeper in the forest (at 30m or 60m depths) in the hotter temperatures than in the cooler temperatures, yet the amount of time they spent at these depths never exceeded the amount of time they spent at their preferred location (edge for NHE 3 and NHE 8, and out for NHE 6 and NHE 9).

One possible explanation for this is that although individuals were spending more time at the edge and outside of the forest than at the 60m depths during the hotter temperatures, they were doing so by spending their time in shady areas. This could be the case specially when we consider that "out" of the forest often included areas such as a covered bridge, or partially roofed outdoor cages. Yellow baboons, do not seek out shade, yet when they encounter shay patches during a hot sunny day, they slow their rate of activity and spend more time in this location (yellow baboons: Stelzner 1988). It is possible, then, that the individuals in our study were employing similar strategies. To analyze if this was the case, we separated our data into clear/scattered days and overcast days. We hypothesized that in clear days, when there are fewer shady patches on the edge of the forest, individuals would spend more time further into the forest as temperatures increase while this preference would not necessarily be apparent during overcast days. What we found is that as the temperature got hotter individuals do spend less time at edge during sunny days, yet they do not spend more time at 60m. Instead, individuals spent more of their time out of the forest as temperatures got hotter. As we expected, during overcast days, the use of edge did not differ greatly for the different temperature categories, yet the use of out of the forest for overcast days also increased as temperatures got hotter. Furthermore, contrary to what we expected, individuals spent more of their time at 60m during overcast days than during sunny days for all temperatures. Future studies could analyze this further by determining if during the hotter days, individuals who were out spent the majority of their time in the sun, in shady areas, or using structures such as the cover bridge or the covered cages.

Another possible explanation for the higher use of out of the forest and the edge over other depths of the forest is human influence. Individuals were often fed at these locations; in fact for enclosures NHE 3 and NHE 6, the feeding stations were located at the edge of the forest. Individuals were also seen anticipating food up to an hour before they were scheduled to be fed, and would remain at the feeding location up to an hour after they were fed. Individuals in enclosures whose feeding stations were not at the edge would also be seen going to the entrance of the outdoor cages where the keepers would come from to feed them in anticipation of being fed. Animals indeed have been seen to use more of the enclosures by going deeper in the forest and higher in the trees in the evenings after the techs have gone home for the da (Digby pers. comm.). This hypothesis, however, would require further data collection and analysis before any conclusive relationships can be drawn.

Previous studies on lemurs and other primates have shown that an important behavioral thermoregulatory strategy is changing postures in response to temperature (Morland 1993, Ostner 2002, and Donati *et al* 2011). Since other lemurs have been seen to increase the rate of hunched postures during colder temperatures, we hypothesized that the individuals of *L. catta* and *P. coquereli* observed in this study would also show an increased rate of tucked postures during colder temperatures and an increased rate of extended postures to facilitate heat dissipation during hotter temperatures (Morland 1993, Ostner 2002, Donati *et al.*

2011). In fact, we found that extended postures were never observed at temperatures below 20°C, and that the amount of time spent in these postures increased as temperatures got hotter, with individuals spending more than 60% of their time in this posture during temperatures between 30.1°C and 35.0°C. As expected, the amount of time spent in tucked postures decreased as temperatures got hotter, with less than 3% in a tucked posture during temperatures between 30.1°C and 35.0°C.

The temperature analysis from the first part of this study showed that the interior of the forest (60m) acts as a sort of buffer from temperature variation, experiencing the least amount of temperature variation than any other depth category explored in this study. Thus, we hypothesized that during each particular temperature category, individuals would spend less of their time adjusting their postural behavior if they were at the interior of the forest than if they were at the edge of the forest where more variation is experienced. Our results were not conclusive as to this effect. We did find that for temperatures between 20.1°C and 30.0°C, individuals at 60m spent less time using extended postures than at the edge, yet for the hottest temperatures (between 30.1°C and 35.0°C) individuals spent more time in an extended posture at edge than at 60m. Similarly for most temperatures, individuals spent less time tucked at 60m than at edge, but for temperatures between 20.1°C to 25.0°C, individuals spent more time tucked at edge.

Overall, individuals of *Lemur catta* and *Propithecus coquereli* did show the employment of behavioral thermoregulatory strategies, such as increased used of extended postures during hotter temperatures and tucked postures during colder temperatures, yet their use of microhabitat selection as a strategy of behavioral thermoregulation remains unclear. Although some of the patterns in the way individuals used the forest were consistent with our hypothesis that as temperatures increased individuals would spend more time in the interior of the forest where perceived temperatures are cooler, these patterns were not always consistent. One possible reason for our inconclusive data is the fact that our temperatures did not vary greatly from the thermoneutral zone of lemurs. Our lowest temperature observed was 12.8°C and the highest temperature was 34.9°C, both of which are less than 10°C from the thermoneutral zone. Furthemore, these extreme temperatures were only observed on a few occasions, and the majority of our data took place during temperatures between 20.0°C and 30.0°C. It is possible that lemurs increase the use of the forest as a thermoregulatory strategy as the ambient temperatures get more extreme, where postural behavior alone may not be enough to maintain a stable body temperature. Another possible caveat of our study is small sample size. Despite having obtained over 226 20-minute focal samples (5200 minutes of data), when analyzing each enclosure separately and separating the data into particular temperature categories, the number of focals per individual was usually about 10 focals. Therefore, future studies that analyze microhabitat selection should aim to obtain data for a greater temperature range and for a longer period of time.

The results of this study suggest that lemurs may use their microhabitat as a strategy for behavioral thermoregulation, although the way they use the forest did not always agree with our expectations. The use of the microhabitat as a behavioral thermoregulatory strategy is an important aspect of behavioral thermoregulation that needs further research because it can provide information as to the effects of deforestation on the ability of the lemurs to regulate their body temperatures, an ability crucial to survival. More specifically, the results of our study suggest that for captive enclosures, such as the natural habitat enclosures at the Duke Lemur Center, the location of feeding stations and the interactions between staff and the animals should be monitored closely because they may also affect the choice of the lemur's location at any given time, and thus their ability to use their habitat to help regulate their body temperature.

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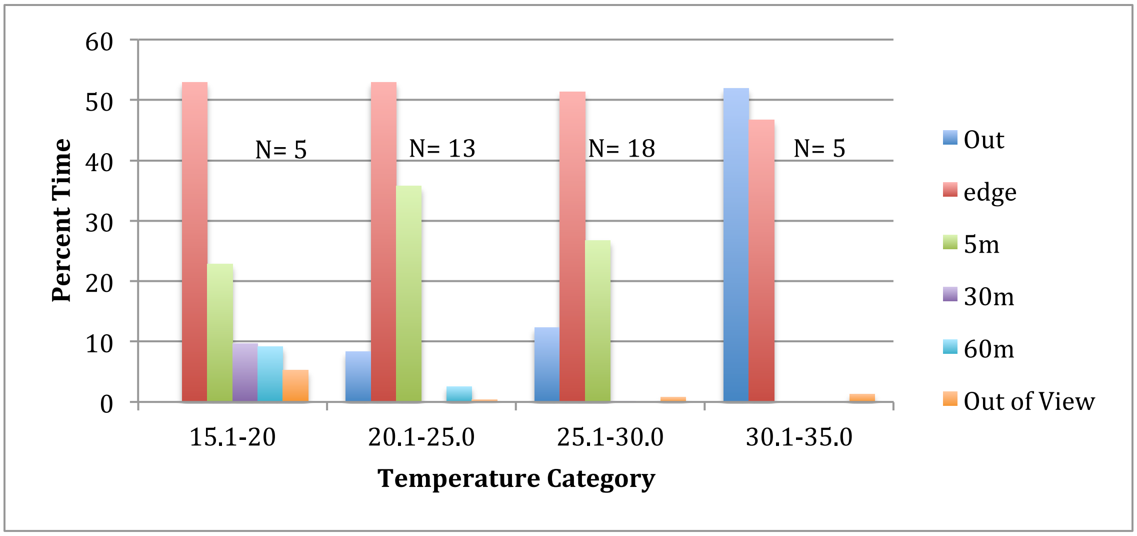
Appendix I: Definition of Behaviors Observed

Behavior		**Definition**
Sit	Seated	Weight resting on haunches with arms resting at sides or on the ground. Ventrum is not opened towards the sun.
	Up-sunning	Weight resting on haunches with ventrum exposed towards sun and arms extended away from torso
	Extended	Weight resting on haunches or lower back with at least one or more limbs extended out, grabbing onto a substrate away from the body. Body orientation tilted back more than other seated postures. Ventrum not exposed to sun.
	Tail Wrap	Body resting on posterior with ventrum either exposed or not exposed. Tail wrapped around the torso. Head and limbs not tucked into the body.
	Tuck	Body resting on posterior with ventrum not exposed, arms and hands tucked in to the body, tail either curled or wrapped around the torso
Cling	Open	Both feet cling onto substrate, holding the weight of the individual. At least one hand holds onto the substrate, keeping the posture upright. Animal is leaning back to expose the ventrum, which is extended away from the substrate.
	Closed	Both feet clinging onto the substrate, holding the weight of the individual. Both hands pull torso into contact with the substrate, ventrum not exposed.
Standing	Stand	Resting with weight supported by hands and/or feet touching substrate and extended
Huddling	Mono	Extensive body contact (such as torso to back or torso to torso) with one conspecific
	Poly	Extensive body contact (such as torso to back or torso to torso) with multiple conspecifics
Suspensory	Towards sun	Hanging from a substrate with at least two hands and/or feet, body opened up so that ventrum is exposed to the sun
	Away from sun	Hanging from a substrate with at least two hands and/or feet, either in the shade or with ventrum facing away from the sun.
Lay		Resting flat on a substrate while on ventrum
Lounge		Resting flat on a substrate on dorsal side with ventrum exposed

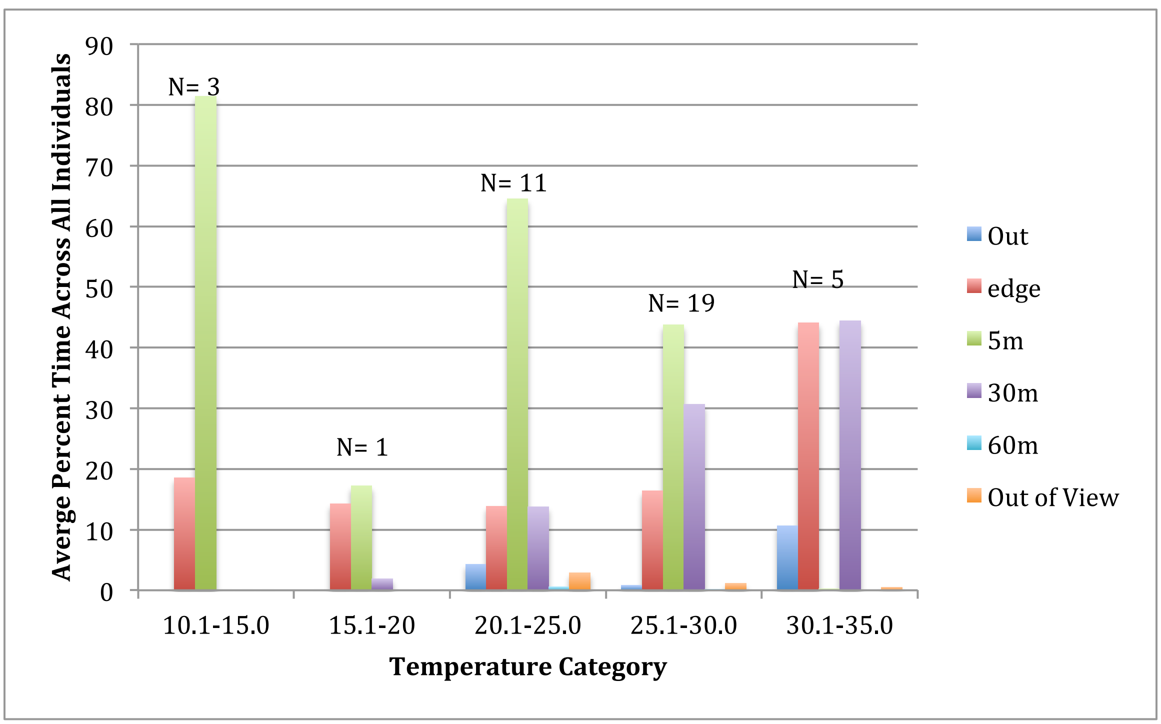
Affiliative	Allogroom	Bouts of running tooth comb through the fur of another individual- could appears as if they are licking them.
	Social Play	Non-aggressive wrestling, jumping on another individual, playful biting, or rolling around with another individual.
Self-Groom		Bouts of running tooth comb through one's own fur- could appear as if animal is licking itself.
Aggression		An instance of a bite, a nip, a quick jab or hit, lunging at another individual, or a series of these actions to show disapproval of a social interaction. Usually accompanied by vocalizations.
Locomotion	Slow	Moderate forward movement such as bipedal galloping or quadrapedal walking (moving forward by alternating one foot and/or hand in front of the other) on the ground or a flat substrate.
	Fast	Rapid forward movement such as fast galloping or running and hopping (simultaneously lifting both hands and/or feet off surface) on the ground or a flat substrate.
	Climb	Moving arboreally or up and down on an artificial substrate, where at least one limb is always in contact with the substrate
	Leap	Fast locomotion between arboreal or artificial substrates where all limbs leave initial substrate contact
Eat		Consuming food
Drink		Consuming water
Lick	Foot licking	Making contact between tongue and bottom or top of foot
	Hand licking	Making contact between tongue and palm or back of hand (sometimes includes wrist/palm combo)
Pant		Open mouth, heavy breathing while the animal is at rest.
Out of View		Subject cannot be seen at all or is too obscured for observer to confidently identify activity
Other		Behavior not identified above

Appendix II



Percent time of each temperature category spent by *Propithecus coquereli* at a given depth. The bars represent what percent of the total observed time at the temperature category individuals spent within a given depth. N is the total number of 20 minute focals that were collected at the given temperature category across the 3 individuals.

Appendix III



Percent time of each temperature category spent by *Lemur catta* at a given depth. The bars represent what percent of the total observed time at the temperature category individuals spent within a given depth. N is the total number of 20 minute focals that were collected at the given temperature category across the 3 individuals.